GROWTH AND NESTLING PERIODS OF CASSIN'S AUKLETS: ADAPTATIONS OF PLANKTIVOROUS AUKLETS TO BREEDING AT NORTHERN LATITUDES

by
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1987

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CANADIAN TECHNICAL REPORT OF HYDROGRAPHY AND OCEAN SCIENCES NO. 93

Canada

88-00073/

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Cat. No. Fs-97-18/93 ISSN 0711-6764

Correct citation for this publication:

Vermeer, K. 1987. Growth and nestling periods of Cassin's Auklets: adaptations of planktivorous auklets to breeding at northern latitudes. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 93: iii + 26 p.

ABSTRACT

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The time of hatching and fledging, growth and nestling period of Cassin's Auklets (Ptychoramphus aleuticus) were investigated in British Columbia and compared with those of Cassin's Auklets in California and planktivorous alcids in Alaska and Svalbard. The nestling stage of Cassin's Auklets in British Columbia was shorter than in California, but their nestling periods were identical. The nestling stage and nestling period of Cassin's Auklets in temperate regions were much longer than those of planktivorous auklets at arctic latitudes. The relatively brief nesting periods of arctic auklets are thought to be adaptations to breeding in regions with abundant but seasonally limited plankton prey, and are made possible by frequent feeding during long daylight hours. The growth form of planktivorous auklets in arctic regions is characterized by a short acceleration phase, a steep linear phase reflecting a high linear growth rate, and a short decelerating phase. High latitude-inhabiting puffins show similar adaptations.

Key words: Cassin's Auklet, growth, nestling stage and period, adaptations.

RÉSUMÉ

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Les périodes d'éclosion, de séjour au nid, de croissance et d'abandon du nid furent déterminées pour l'Alque de Cassin (Ptychoramphus aleuticus) nichant en Colombie Britannique. Ces données sont comparées à celles sur l'Alque de Cassin nichant en Californie et à celles sur d'autres espèces d'alques planctivores nichant en Alaska et au Svalbard. La période de nidification de l'Alque de Cassin était moins longue en Colombie Britannique qu'en Californie, alors que la durée de séjour au nid des jeunes était identique. Dans les régions tempérées, les périodes de nidification et de séjour au nid chez l'Alque de Cassin étaient plus longues que celles des alques planctivores nichant à des latitudes arctiques. On croit que la durée relativement courte du séjour au nid des alques planctivores de l'Arctique est une adaptation à la reproduction dans les régions ou le plancton n'abonde que d'une façon très saisonnière. Cela est possible à cause des longues journées polaires qui permettent une alimentation plus fréquente. Chez les alques planctivores des régions arctiques, la courbe de croissance est caractérisée par une courte phase de croissance accélérée, suivie d'une phase linéaire à pente abrupte qui marque un taux de croissance linéaire élevé et, finalement, par une courte phase de croissance ralentie. Les macareux vivant à des latitudes élevées montrent des adaptations semblables.

Mots-clés: alque de Cassin, croissance, la période de nidification, la durée du séjour, adaptations.

INTRODUCTION

There are five species of planktivorous auklets in the North Pacific Ocean; the Cassin's (Ptychoramphus aleuticus), Crested (Aethia cristatella), Least (A. pusilla), Parakeet (Cyclorrhynchus psittacula) and Whiskered (A. pygmaea) auklets. The Dovekie (Plautus alle) is found in the North Atlantic and Arctic oceans. All those species raise one nestling per breeding pair in a nest burrow, and possess a gular pouch, which serves as a food storage receptacle for feeding nestlings (eg. Speich and Manuwal 1974, Vermeer 1984, Vermeer et al. 1987). Those auklets also have relatively wide beaks and broad fleshy tongues which facilitate feeding on zooplankton (Bédard 1969).

The objective of this paper is to document the duration of the nestling stage (time of year when hatching and fledging occurred), growth and nestling period (average time interval between the hatching and fledging of a chick) of Cassin's Auklets in British Columbia and compare them with those of Cassin's Auklets in California and other planktivorous auklets in Alaska and Svalbard, to determine whether auklets at northern latitudes differ in nestling period and growth from those breeding farther south. For that purpose I studied the growth and nestling periods of Cassin's Auklets on Triangle Island (50°52'N, 125°05'W) in 1978 and on Frederick Island (53°56'N, 133°10'W) in 1980 and 1981 (Fig. 1). Some aspects of Cassin's Auklet growth on Triangle Island have been previously reported by Vermeer (1981) and Vermeer and Cullen (1982). Growth and nestling periods have been investigated for Dovekies (Norderhaug 1980), Least Auklets (Sealy 1968, Searing 1977, Roby and Brink 1986), Crested Auklets (Sealy 1968), Parakeet Auklets (Sealy 1968, Sealy and Bédard 1973, Searing 1977). The hatching and fledging times of Whiskered Auklets are only approximately known (Knudtson and Byrd 1980).

The present report complements information on the nestling diet of Cassin's Auklets on Frederick and Triangle Islands, published in this report series (No. 56) by Vermeer (1985).

STUDY AREA AND METHODS

The study areas of Triangle and Frederick islands have been previously described by Vermeer et al. (1976, 1984). To determine the nestling stage, the calendar duration of hatching and fledging of Cassin's Auklets was recorded. The nestling period was determined by measuring the intervals between the time of hatching and fledging of nestlings to the nearest day. The procedure of checking nest burrows has been described by Vermeer (1981).

To determine growth of Cassin's Auklets, nestlings were weighed daily with 100 and 300 g Pesola scales (Frederick Island, 1980 and 1981) and on alternate days (Triangle Island, 1978). In addition, chicks close to fledging were weighed on Triangle Island in 1982, to determine departure dates and fledging weights. Tarsus length of nestling Cassin's Auklets were measured on Frederick Island with calipers to the nearest 0.1 mm. Weight increments of nestling Cassin's Auklets on Triangle Island have been previously published (Vermeer, 1981). Sample sizes and weight increments of nestling Cassin's Auklets collected on Frederick Island are summarized in Appendices 1 and 2. Those appendices are very important for comparison since greatly reduced figures of growth curves that have appeared in major journals without supportive data have been a source of frustration and are of limited value, if not completely worthless, for that purpose.

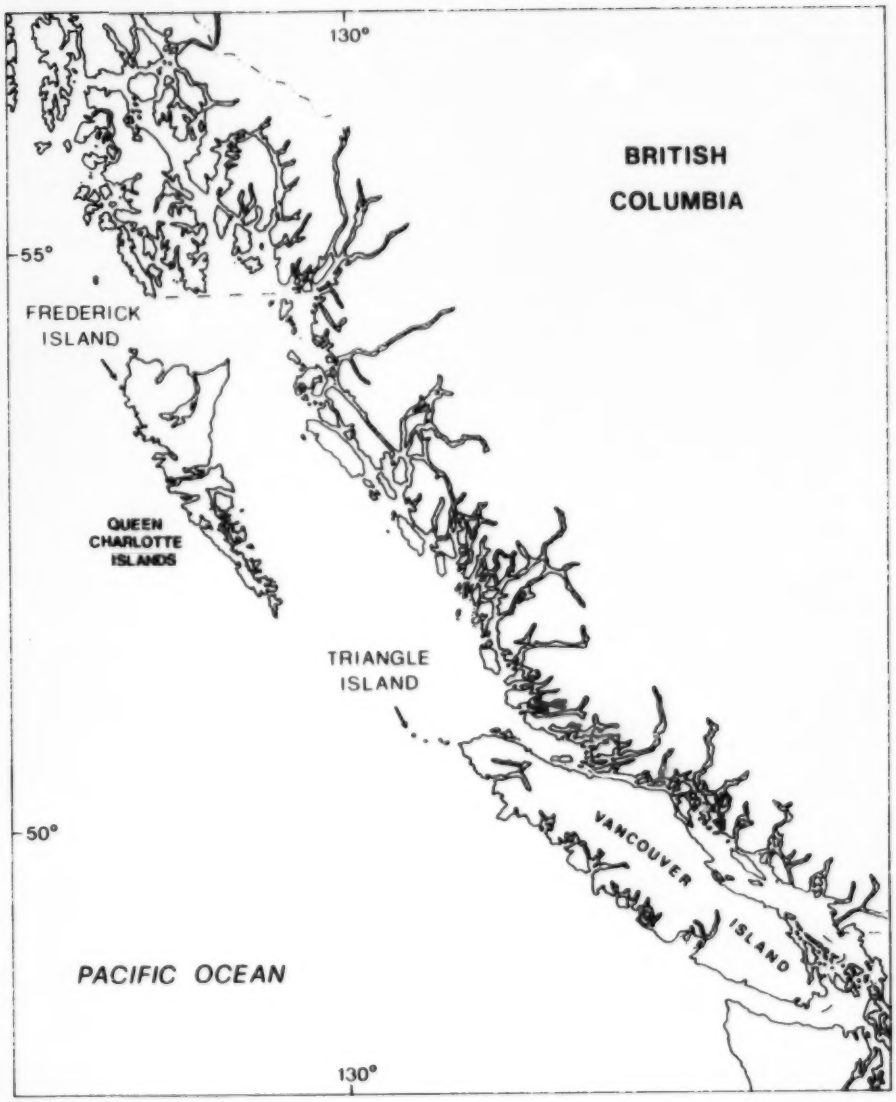

Figure 1 Location of Frederick and Triangle Islands, British Columbia.

Average seawater temperatures were compared for the month of May between Frederick and Buldir Islands, since they occur at similar latitudes and as both have nesting populations of Cassin's Auklets. Climatic conditions however, vary between the islands; Frederick Island has a temperate climate and Buldir Island a subarctic one. I obtained 1974-1985 seawater temperature data from the light-station at Langara Island, 37 km north of Frederick Island, and from Adak Island (51°45'N, 176°45'E) in the Aleutians. Langara Island is the closest location to Frederick Island, and Adak Island to Buldir Island where seawater temperatures are recorded.

RESULTS

1. Chronology of hatching and fledging

Mean hatching dates of nestling Cassin's Auklets fell on 26 May on both Triangle Island in 1978 and on Frederick Island in 1980 (Table 1). In 1981, the mean hatching date on Frederick Island fell on 3 June, which was significantly later than 1980 ($t_2(179) = 7.26$, $P<0.005$). Nestlings on Triangle Island fledged on the average on 11 July in 1978, and on Frederick Island on 12 and 17 July in 1980 and 1981, respectively. Cassin's Auklets fledged significantly later on Frederick Island in 1981 than in 1980 ($t_2(102) = 6.99$, $P<0.005$). Prolonged hatching on Triangle Island in 1978 and on Frederick Island in 1980 resulted in extended fledging (Fig. 2). On the other hand, the relatively brief hatching period on Frederick Island in 1981, resulted in contracted fledging which made those two periods distinct from one another (Fig. 2). The mean age at fledging (identical to the nestling period) was 44 to 45 days (Table 1), and ranged from 40 to 57 days.

2. Weight recession and variation in growth

Nestling Cassin's Auklets reached an average maximum or peak weight 7.5 days prior to fledging (mean ± SD: 7.5±3.6 d, n=101). On reaching peak weight the nestlings were heavier than at fledging (Fig. 3). Peak and fledging weights declined over the nestling season (Table 2) and varied among nestlings from 155 to 245 g and from 155 to 220 g, respectively (Fig. 3). Peak and fledging weights were positively correlated with one another (r=0.772).

On Frederick Island, early and late hatched nestlings had similar rates of weight increments during their first two weeks of life. However, between two and four weeks of age late-hatched nestlings were heavier and at fledging lighter again than early-hatched Cassin's Auklets (Fig. 4). On Triangle Island, early-hatched Cassin's Auklets were also heavier than late-hatched ones at the time of fledging (Table 2).

Weight increments of nestling Cassin's Auklets are compared between Frederick, Triangle and South Farallon islands in Fig. 5. The growth curve for Cassin's Auklets at South Farallon Island is derived from data by Thoresen (1964), and is similar to that reported there in 1970 by Manuwal (1974), which suggests that the growth curve at South Farallon Island is typical for the species at that location. On Frederick Island, nestlings were on the average heavier in 1980 than in 1981. Weight increments of nestlings on Frederick Island in both years were considerably above those on Triangle Island, and the latter in turn above those of South Farallon Island (Fig. 5). The growth comparison suggests that nestling Cassin's Auklets are heavier at northern

Table 1. Comparison of hatching and fledging dates and age at fledging of nestling Cassin's Auklets on Triangle and Frederick Islands, 1978-1982 (sample number in parentheses)

Age and time of hatching and fledging	Mean and standard deviation			
	Triangle Island		Frederick Island	
	1978	1982	1980	1981
Hatching date	May 26.6±10.9(74)	-	May 26.2± 9.4(81)	June 3.7±6.1(100)*
Fledging date	July 11.1±10.3(48)	July 9.0±9.2(67)	July 12.0±10.4(49)	July 17.1±6.2(52)*
Age of fledging (days)	44.1± 3.9(48)	-	45.0± 2.5(49)	43.8±6.3(52)

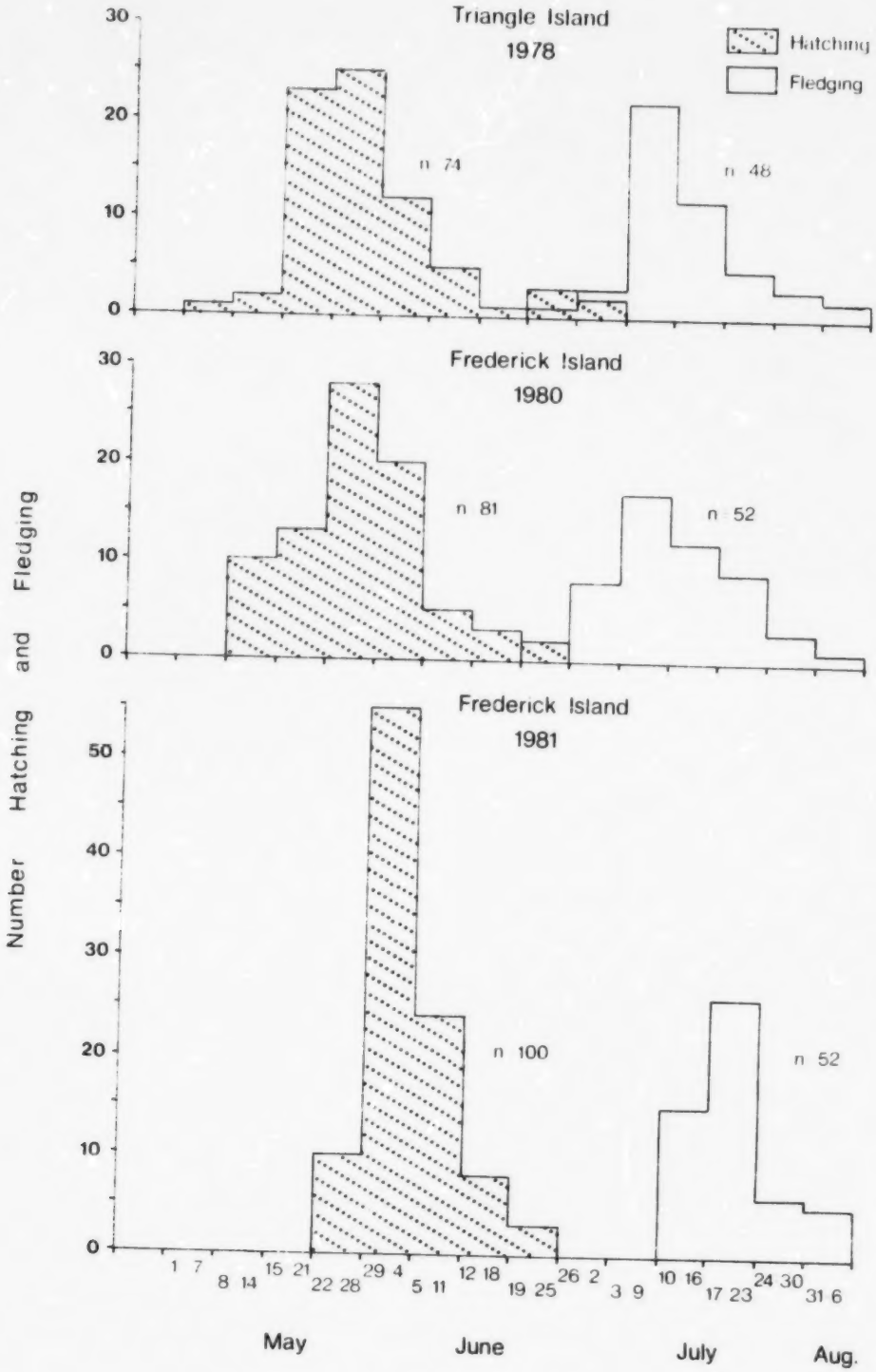

Figure 2 Comparison of hatching and fledging times of nestling Cassin's Auklets on Triangle Island in 1978 and on Frederick Island in 1980 and 1981.

Table 2. Comparison of peak and fledging weights of nestling Cassin's Auklets on Triangle and Frederick Islands, 1978-1982 (sample number in parentheses)

Peak and fledging weights at different times of the nesting period	Mean and 95% confidence intervals			
	Triangle Island		Frederick Island	
	1978	1982	1980	1981
Peak weights (grams)				
June 17-30	191.0±12.8(2)	-	218.2±7.9(9)	-
July 1-14	192.4±6.3(19)	-	201.9±5.6(27)	202.5±11.9(11)
July 15-31	180.3±19.1(4)	-	200.0±9.5(13)	198.8±5.1(35)
July 29-August 6	-	-	-	178.8±15.3(6)
Overall average	190.4±5.4(25)	-	204.4±4.4(49)	197.2±4.6(52)
Fledging weights (grams)				
June 17-30	174.4±13.0(3)	169.9±8.0(10)	194.9±10.6(9)	-
July 1-14	170.8±4.4(35)	160.0±5.2(38)	177.4±6.4(27)	171.5±8.2(11)
July 15-31	158.7±15.7(6)	161.5±10.3(19)	171.8±7.8(13)	169.7±4.4(35)
July 29-August 6	164.0±10.4(4)	-	-	143.7±20.3(6)
Overall average	167.9±3.7(48)	161.9±4.2(67)	179.1±4.8(49)	167.1±4.4(52)

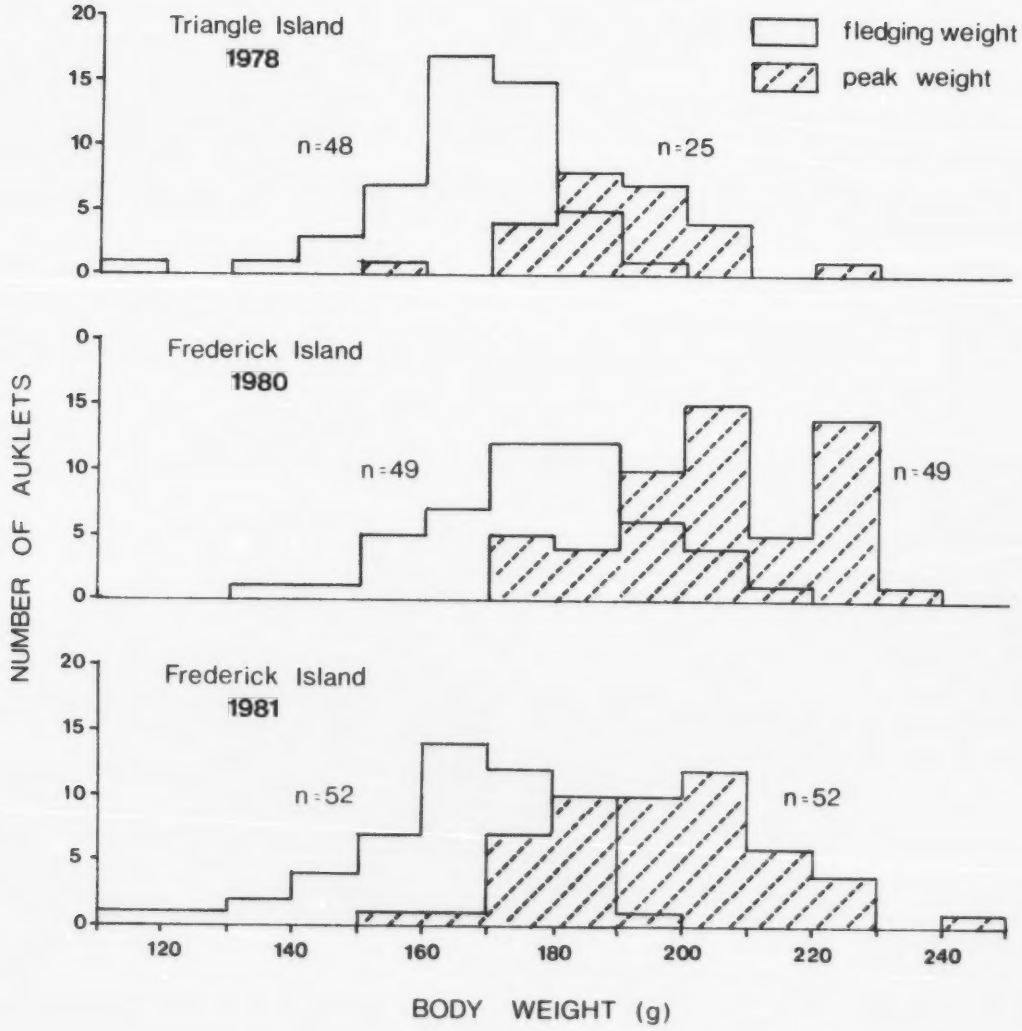

Figure 3 Disbtribution of fledging and peak weights of nestling Cassin's Auklets on Triangle Island in 1978 and on Frederick Island in 1980 and 1981.

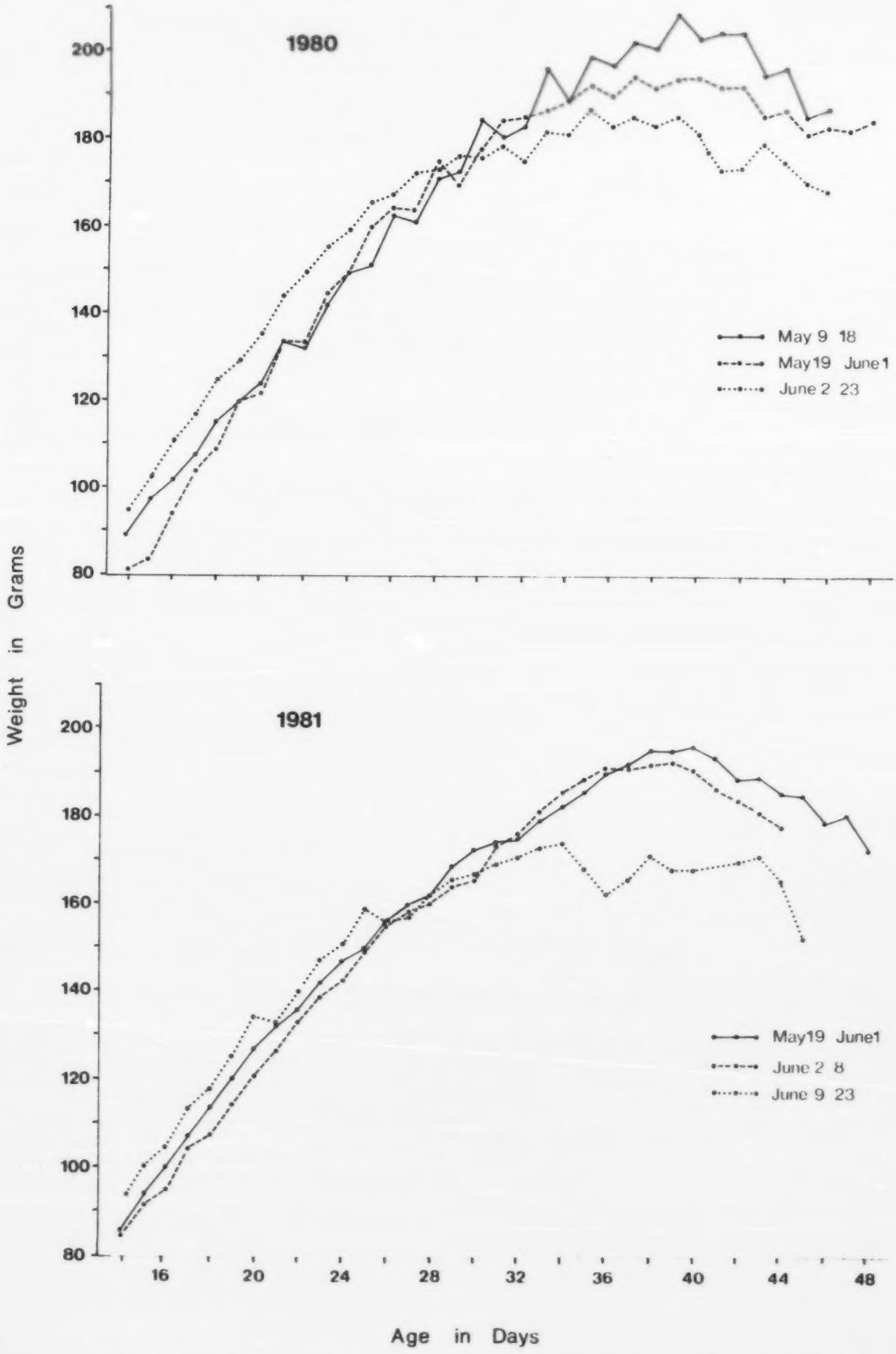

Figure 4 Comparison of weight increments of nestling Cassin's Auklets hatched during different time periods, May 9-18, May 19-June 1, June 2-8 and June 9-23, on Frederick Island. The June 2-8 and 9-23 periods have been combined in a June 2-23 period for 1980 because of small sample size for the separate periods.

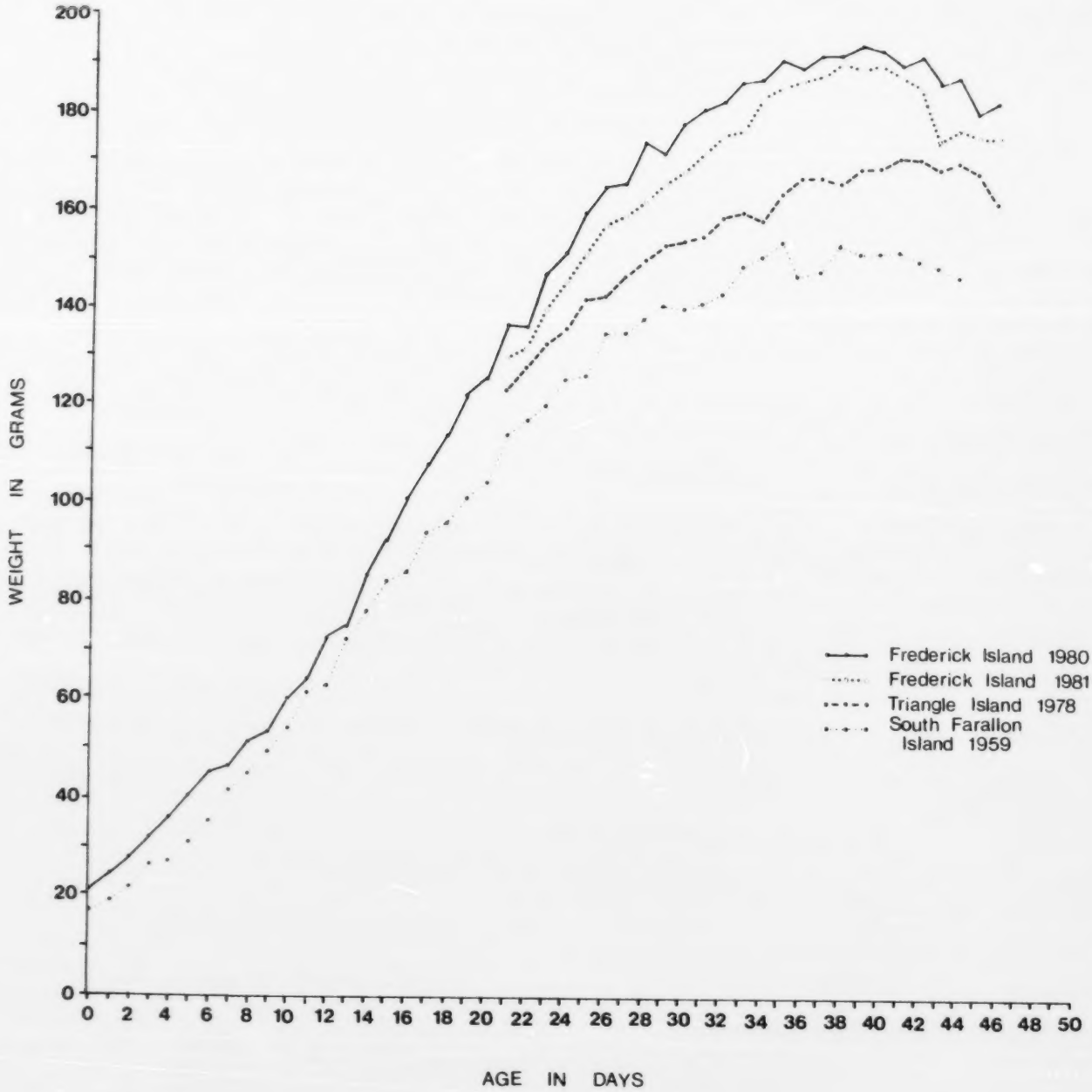

Figure 5 Comparison of weight increments of nestling Cassin's Auklets on Frederick Island in 1980 and 1981, on Triangle Island in 1978, and on South Farallon Island in 1959 (Thoresen 1964). Increments are only shown for nestlings three weeks and older on Frederick Island in 1980 and on Triangle Island in 1978 as nestlings' weights prior to three weeks of age did not differ much from those on Frederick Island in 1981.

latitudes. Although nestling Cassin's Auklets were heavier in British Columbia than in California, tarsus measurements, which are less susceptible to differences in seasonal food conditions than body weights, suggest that nestlings in the two regions may be identical in body size (Table 3).

3. Growth curves of planktivorous auklets

Growth curves of planktivorous auklets are compared on a relative basis in Fig. 5, i.e., as a percentage of adult weight (Table 4), to eliminate size differences between species. Growth curves of nestlings up to three weeks of age of Cassin's Auklets on Triangle Island in 1978, on Frederick Island in 1981, and on South Farallon Island in 1959 (Thoresen 1964) are omitted from Fig. 6 for purposes of clarity. Similarly, that of the Parakeet Auklet on St. Lawrence Island in 1967 is not included in Fig. 6. However, the relatively small sample size of the Parakeet Auklet suggests a similar growth curve to that of the Crested Auklet (Sealy 1968). Weight increments of nestling Crested and Least auklets are representative of the largest and smallest planktivorous auklets, respectively (Table 4) and have been combined for each species for 1966 and 1967 to increase sample size (for sample size, see Sealy 1968). The combined 1963 and 1964 growth curve of the Dovekie on Svalbard is derived from Norderhaug (1980).

Growth curves shown in Fig. 6 are representative of auklets inhabiting different environments. The Cassin's Auklet is chiefly a northern temperate species, Crested and Least auklets are low arctic species, and the Dovekie is a high arctic species. Fig. 6 shows that Dovekies, Crested and Least auklets do not only have much shorter growth periods but also an initially briefer accelerating phase, a steep linear phase and a much shorter decelerating phase than the Cassin's Auklet. Without calculating actual linear growth rates, it can be seen from Fig. 6 that the Least Auklet had the highest linear growth rate followed by the Dovekie and the Crested Auklet, which in turn had higher rates than the Cassin's Auklet.

DISCUSSION

4. Nestling period and its calendar duration

Nestling periods and the nestling stage are known and are compared to latitudes where they occur in Table 5. Cassin's Auklets had the longest nestling periods of the six species. Those periods (41-45 days) were similar for Cassin's Auklets at 37° and 54°N, which suggests that latitudinal range does not affect the length of the nestling period. Cassin's Auklets started hatching in both California and British Columbia in May, but the calendar range of the nestling stage was much longer in California than in British Columbia (Table 5).

Least, Whiskered and Crested auklets on Buldir Island (52°21'N, 175°56'E), which is at a slightly lower latitude than Frederick Island (53°56'N), hatched about one month later than Cassin's Auklets on Frederick Island, suggesting that latitude per se does not govern the initiation of hatching and duration of the nestling period of auklets at 52-54°N latitude. Sea-surface water in the Buldir Island region averaged 4.5°C and near Frederick Island 8.8°C during May 1975-1984. Colder seawater and therefore a likely later availability of plankton prey to nestling auklets at Buldir than Frederick Island may delay breeding at Buldir Island. Birkhead and Harris (1985) also reported a weak

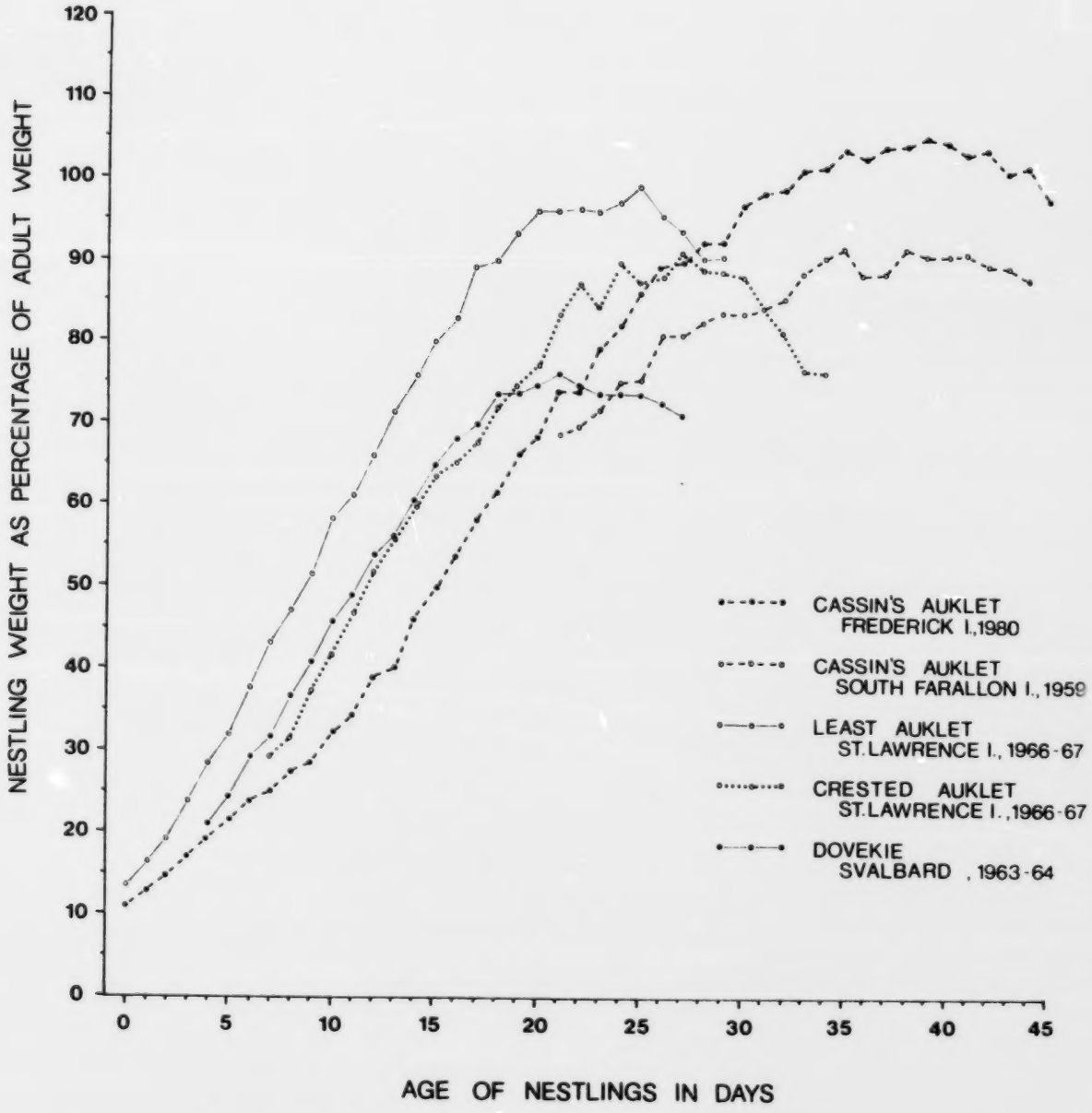

Figure 6 Comparison of weight increments of nestlings as a percentage of adult weight of Cassin's Auklets on Frederick Island (1980) and on South Farallon Island (1959) with those of Crested and Least auklets on St. Lawrence Island (1966 and 1967) and the Dovekie on Svalbard (1963 and 1964).

Table 3. Comparison of tarsus length of nestling Cassin's Auklets on Frederick Island, 1981, and on South Farallon Island, 1959 (Thoresen 1964)

Age in Days	Frederick Island		South Farallon Island	
	Number of nestlings	Mean and SD(mm)	Number* of nestlings	Mean (mm)
0	14	16.6 ± 0.5	11	16.6
1	14	16.8 ± 0.7	13	17.4
2	16	17.7 ± 0.7	13	17.9
3	16	18.0 ± 0.7	8	18.2
4	16	18.9 ± 0.7	10	18.9
5	16	19.6 ± 0.8	10	19.2
6	16	20.0 ± 1.2	10	19.9
7	16	20.2 ± 1.2	7	20.0
8	16	20.9 ± 1.0	7	21.1
9	15	21.2 ± 1.2	10	22.0
10	16	21.7 ± 1.3	10	22.4
11	15	22.2 ± 1.3	9	22.6
12	15	22.2 ± 1.4	9	22.9
13	15	22.6 ± 1.5	8	22.9
14	16	22.9 ± 1.3	7	23.2
15	16	23.3 ± 1.2	10	23.8
16	16	23.4 ± 1.3	11	24.2
17	16	23.7 ± 1.1	9	24.7
18	16	24.2 ± 1.3	9	24.7
19	16	24.2 ± 1.2	9	24.9
20	16	24.6 ± 1.1	10	25.1
21	16	24.9 ± 1.2	9	25.3
22	16	25.0 ± 1.3	9	25.5
23	16	25.5 ± 1.2	9	25.9
24	16	25.4 ± 1.1	8	26.2
25	14	25.8 ± 1.0	9	26.4
26	16	25.8 ± 1.2	10	26.6
27	16	25.9 ± 1.2	11	26.6
28	16	25.9 ± 1.0	9	26.8
29	16	26.1 ± 1.0	10	26.8
30	16	26.1 ± 0.9	9	26.9
31	15	26.2 ± 1.0	11	27.1
32	15	26.2 ± 0.8	11	27.2
33	15	26.2 ± 0.8	11	27.2
34	15	26.5 ± 1.0	11	27.2
35	16	26.4 ± 1.0	11	27.3
36	15	26.5 ± 0.8	10	27.4
37	16	26.5 ± 0.8	12	27.4
38	15	26.4 ± 0.8	12	27.4
39	15	26.4 ± 0.7	12	27.4
40	14	26.4 ± 0.8	11	27.4
41	11	26.5 ± 0.6	11	27.5
42	10	26.5 ± 0.8	8	27.5
43	8	26.6 ± 0.7	9	27.6
44	6	26.6 ± 0.9	6	27.3
Adults	6	26.9 ± 0.8	21	26.6

* Thoresen started with 1 day of age

Table 4. Interspecific differences of nestling and adult weights of auklets (sample number where known in parentheses)

Species, Location, sources	Mean weights (g)			
	Adult	Hatching	Peak	Fledging
Least Auklet, St. Lawrence Is., Alaska Sealy 1968	92 (125)	12.3(32)	91	81(25)
Dovekie, Spitsbergen Norderhaug 1980	163.5(74)	21.5(84)	125*	114(41)
Cassin's Auklet, South Farallon Is., California Thoresen 1964, Manuwal 1974	168(4438)	18 (11)	154*(11)	149 (9)
Cassin's Auklet, Triangle Is., B.C., this study	185(31)**	21.4(8)	190 (25)	168(48)
Cassin's Auklet, Frederick Is., B.C., this study	185(31)**	20.5(23)	200(101)	173(111)
Crested Auklet, St. Lawrence Is., Alaska, Sealy 1968, 1973	287(192)	29.5(13)	254	228(15)
Parakeet Auklet, St. Lawrence Is., Alaska, Sealy 1968, Sealy and Bédard 1973	281(17)	28(4)	239	223(6)

* Estimated from growth curves in literature
** Combined for Triangle and Frederick Islands

Table 5. Comparison of nestling periods and their duration for auklets

Species, location and sources	Latitude (to nearest) degree N	Mean nestling period (days) N	Mean nestling period (days) x	Duration of nestling stage N	Duration of nestling stage Calendar range	Duration of nestling stage Days
Cassin's Auklet, S. Farallon Is. California, Thoresen 1964	37°	17	45	-	? May-18 Aug., 1959	-
Cassin's Auklet, S. Farallon Is. California, Manuwal 1974, Speich and Manuwal 1974	37°	16	41	-	14 May-15 Sept., 1970	124
Cassin's Auklet, Triangle Is. B.C., this study	51°	48	44	48	7 May-2 Aug., 1978	87
Cassin's Auklet, Frederick Is. B.C., this study	54°	49	45	49	10 May-1 Aug., 1980	83
		52	44	52	27 May-3 Aug., 1981	68
Least Auklet, Buldir Is., Alaska, Knudtson and Byrd 1982	52°	-	-	-	24 June-22 Aug., 1974-1976	59
Least Auklet, St. George Is., Alaska, Roby and Brink 1986,	56°	20	28.6	-	27 June-15 Aug., 1981-1982	49
Least Auklet, St. Lawrence Is., Alaska, Sealy 1968,	64°	20	29	17	15 July-1 Sept., 1966	42
Crested Auklet, Buldir Is., Alaska, Knudtson and Byrd 1982	52°	-	-	-	1 July-22 Aug., 1974-1976	56
Crested Auklet, St. Lawrence Is., Alaska, Sealy 1968	64°	16	33.5	11	21 July-10 Sept., 1966	42
Whiskered Auklet, Buldir Is., Alaska, Knudtson and Byrd 1982	52°	-	-	-	24 June-22 Aug., 1974-1976	59
Parakeet Auklet, St. Lawrence Is., Alaska, Sealy and Bédard 1973	64°	6	35	6	24 July-7 Sept., 1967	45
Dovekie, Norderhaug 1980	77°	34	27	34	11 July-18 Aug., 1963	38
				35	16 July-25 Aug., 1964	40

relationship between time of breeding and latitude, but a marked one between sea-surface temperatures and time of breeding for Atlantic alcids.

5. Weight recession and growth variation

Seasonal variation in growth of nestling Cassin's Auklets (Fig. 4) is likely related to prey availability. Meal sizes of nestling Cassin's Auklets often varied significantly over the nestling season (Vermeer 1984, 1985). Several previous studies on planktivorous alcids, such as the Cassin's Auklet (Manuwal 1979, Vermeer 1981, Vermeer and Cullen 1982) and Least Auklets (Sealy 1981) showed that early-hatched chicks were significantly heavier at the time of fledging than those which hatched later. Nestlings of piscivorous alcids that hatched later also grew more slowly and fledged at lighter weight than those that hatched early (Belopolskii 1957, Nettleship 1972, Wilson 1977, Hedgren and Linman 1979, Gaston and Nettleship 1981). All authors argued that those differences in growth rates reflected a decrease in the quality and availability of prey species later in the nestling season.

The heavier nestling Cassin's Auklets on Frederick Island in 1980 than 1981 may reflect annual variation in the amount of food nestlings receive, while the observation of heavier nestlings in British Columbia than in California may relate to auklets in British Columbia being predominantly fed with the high energy copepod, Neocalanus cristatus, which does not appear to be available to nestlings in California (Vermeer 1981, 1984). The presence of heavier nestlings on Frederick Island than on Triangle Island in turn may relate to nestling Cassin's Auklets consuming much greater quantities of Neocalanus cristatus on the former (46 and 44% wet weight of prey in 1980 and 1981, respectively) than on the latter island (23 and 27% wet weight of prey in 1980 and 1981, respectively)(Vermeer 1984).

6. Adaptations to nesting at northern latitudes

No other planktivorous auklet breeds over such an extensive latitudinal range than the Cassin's Auklet, and hence the species lends itself to size comparisons over the range. Although nestlings were heavier, nestling periods of Cassin's Auklets were similar in British Columbia and California but calendar duration of the nestling stage was much more prolonged in California than British Columbia. The shorter nestling season in British Columbia relates to a shorter growing season there than in California, which in turn may determine the duration of zooplankton availability to Cassin's Auklets. A small population of Cassin's Auklets also nests on Buldir Island in the Aleutians (Sowls et al. 1978) but, unfortunately, no data exists on the nestling period. However, it is unlikely that it differs from that on Frederick Island, as its length is the same over the extensive range from British Columiba to California. From the late start of the nestling stage of the other planktivorous auklets on Buldir Island (Table 5) one may predict, however, that Cassin's Auklets will also nest later there than on Frederick Island.

Cassin's Auklets generally breed considerably farther to the south than the low arctic Aethia and Cyclorrhynchus species (see Sowls et al. 1978) and visit their breeding grounds during darkness. This nocturnal rhythm probably is an adaptation to reduce avian predation (eg. see Bédard 1967, Sealy 1973, Vermeer 1979), which is extensive at temperate latitudes (eg. see Vermeer et al. 1984). Predation on auklets may not be less extensive in arctic environments, but the

presence of distinct periods of darkness during summer at temperate latitudes allows the Cassin's Auklet to make use of those periods to visit the colony to reduce avian predation. However, Cassin's Auklets may pay a price for feeding their nestlings at night, i.e. each parent feeds its nestling only once during darkness (Thoresen 1964), while the other five planktivorous auklet species in arctic environments feed their nestlings much more frequently during daylight (eg. see Sealy 1973, Vermeer et al. 1987). Frequent feeding during long daylight hours may allow for briefer growth periods in diurnal arctic and subarctic alcids.

Sealy (1973) suggested that the lower growth rates of nocturnal alcids resulted from lower feeding rates. Roby and Brink (1986), on the other hand, postulated that the growth rate of auklets is not limited by the amount of food adults can deliver to nestlings, based on their observation that nestling Cassin's Auklets consumed twice as much as Least Auklets per day. However, the average daily consumption rate of nestling Cassin's Auklets, on which Roby and Brink (1986) based their comparison, was probably much too high and was not representative of the overall nestling period of Cassin's Auklets as they were collected only at one time period (D.A. Manuwal pers. comm., Vermeer 1981, see also Vermeer 1984, 1985). Sealy's (1973) suggestion therefore has not been proven to be incorrect. Roby and Brink (1986) further postulated that the cost of increased precocity in nestling nocturnal alcids (Cassin's Auklet) may be slower growth rates and longer nestling periods relative to diurnal alcids. Roby and Brink's postulation was based on the assumption that diurnal brooding of Cassin's Auklets abruptly ceases once nestlings are five to six days old, and thermoregulatory development is presumably more precocious. However, the extent of diurnal brooding in Cassin's Auklets does not cease abruptly when nestlings are five to six days old and is not unlike that in diurnal auklets (cf. Norderhaug 1980, Roby and Brink 1986, Vermeer and Lemon 1986).

The relatively brief nestling periods of arctic auklets compared to that of the Cassin's Auklet are thought to be adaptations to breeding in regions with an abundant but compressed supply of plankton prey. The short accelerating phase, the steep linear phase, and the short decelerating phase of the growth curve is characteristic for plantivorous auklets breeding at northern latitudes. Besides adaptations to arctic conditions, smaller species of closely related birds generally develop faster than heavier ones (Ricklefs 1973). Among planktivorous auklets in arctic regions the Least Auklet, the smallest species, had a higher linear growth rate than the larger Dovekie, Crested and Parakeet auklets. Gaston (1985) found that the smallest Atlantic alcid, the Dovekie, had the highest growth rate in Atlantic Alcidae. The high growth rates of small alcids may be a response to greater energy expenditure in small birds because of their greater surface volume ratio (Kendeigh 1970).

7. Comparison with puffins

Further comparisons are made here between the growth and nestling periods of planktivorous auklets and a group of piscivorous alcids, the puffins. The comparison is made as the growth of three puffin species, the Horned Puffin (Fratercula corniculata), the Tufted Puffin (F. cirrhata) and the Rhinoceros Auklet (Cerorhinca monocerata) have recently been documented in British Columbia and in the Gulf of Alaska, and as one species, the Rhinoceros Auklet, has a similar mode of nesting to the Cassin's Auklet, i.e., it feeds its nestling once or twice during darkness in the nest burrow until fledging (Richardson 1961).

Horned and Tufted puffins, like the diurnal planktivorous auklets, feed their nestlings several times per day during daylight (Vermeer 1979, Wehle 1983). In the northeastern Pacific Ocean, the Rhinoceros Auklet has its breeding centre, like the Cassin's Auklet, in the temperate zone from southern Alaska to Washington State (Vermeer 1979), while the vast majority of Horned and Tufted puffins breed to the north of that region in Alaska and in the Pacific U.S.S.R. (Sowls et al. 1978, Vermeer 1979). Unlike the diurnal planktivorous auklets, however, small populations of Horned Puffins nest south to southeastern Alaska and northern British Columbia (Sowls et al. 1978, Campbell et al. 1979) and small to moderate populations of Tufted Puffins breed as far south as California (Ainley and Lewis 1974).

Growth curves of the three North Pacific puffin species are compared in Fig. 7. Like the nocturnal Cassin's Auklet, the Rhinoceros Auklet has a long decelerating growth phase (cf. Figs. 6 and 7). With respect to the length of the nestling period, that of the Rhinoceros Auklet averages longer than that of the Horned and Tufted puffins (Table 6). There appear to be therefore similar adaptive trends in the growth forms and nestling periods of puffins and planktivorous auklets for breeding under arctic conditions.

A compressed nestling period has also been observed in temperate Sulidae compared to those nesting in the tropics. Nelson (1966) reported a 14-week growth period of the Gannet (Sula bassana) in temperate waters and a 30-week period in boobies in the tropics, and he suggested that the compressed growth of the Gannet was an adaptation to utilize a seasonal food supply.

ACKNOWLEDGEMENTS

I thank M. Lemon, T. Carson and D. Herlinveaux for assistance with the field studies on Frederick Island and M. Cullen and R. Billings with that on Triangle Island. R.W. Butler, R.H. Drent and L. Giovando reviewed a preliminary version of this manuscript and made pertinent comments. K. Devito drafted most figures. S.G. Sealy provided a copy of his M.Sc. thesis with growth data on Least, Crested and Parakeet auklets. J.P. Savard prepared the French abstract. L. McDonald typed the manuscript. The Canadian Coast Guard, Prince Rupert, transported the field crew and equipment on its first journey to Frederick Island. The study on Triangle and Frederick Islands was sponsored and financed by the Canadian Wildlife Service.

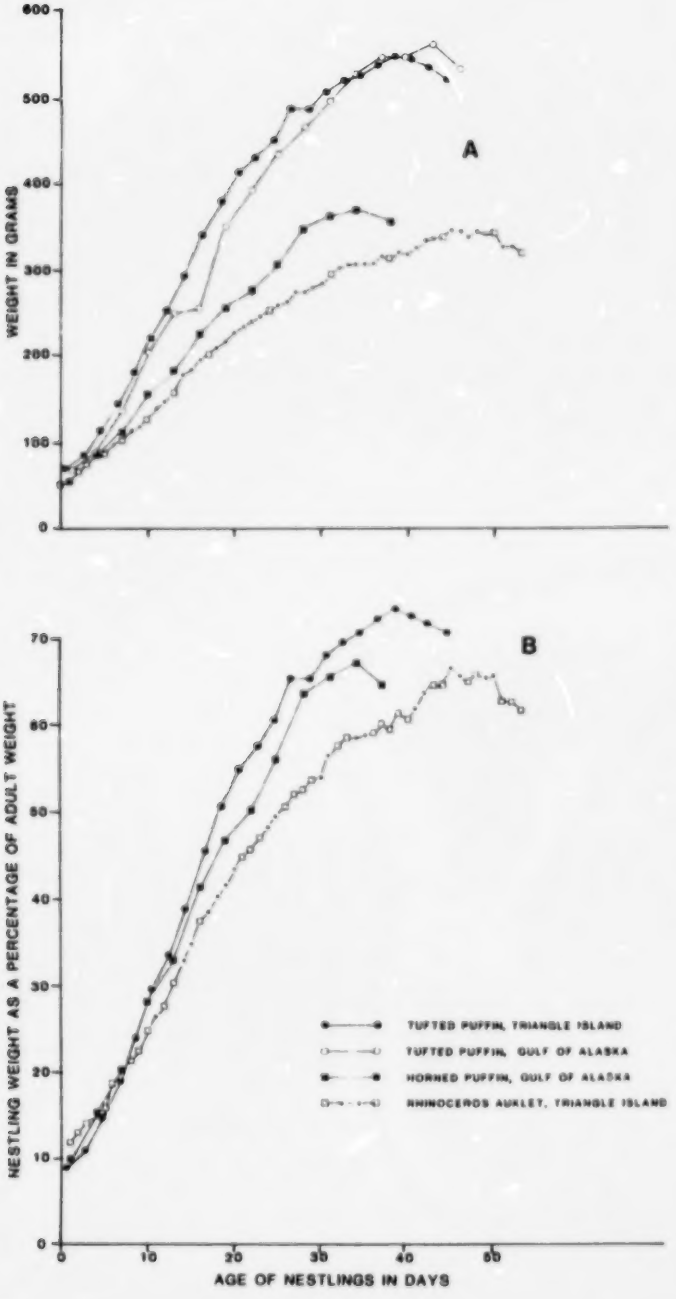

Figure 7. A. Comparison of weight increments of nestling Horned and Tufted puffins in the Gulf of Alaska (Horned Puffin: combined data from Shumagin Islands 1976, Ugaiushak Island 1977, Barren Islands 1977 and Tuxedni Bay 1978; Tufted Puffin: combined data from five sites, Baird and Gould 1983), and those of Rhinoceros Auklets (average of morning and evening weights, Appendix 3) and Tufted Puffins (Appendix 4) on Triangle Island, British Columbia, 1978 (Vermeer unpubl. data).

B. Same data as in A, but presented as a percentage of adult weight. Growth curve of Tufted Puffins in Alaska has been omitted for purpose of clarity and as growth of that species was similar in the Gulf of Alaska and on Triangle Island, British Columbia.

Table 6. Comparison of nestling periods and weights of Horned Puffins, Tufted Puffins and Rhinoceros Auklets (sample number where known in parenthesis)

Species, location, sources	Latitute to nearest degree	Mean Nestling periods (days)	Mean weights (grams)			
			Adult	Hatching	Peak	Fledging
Horned Puffin, Gulf of Alaska Baird and Gould 1983	57°N[a]	42(12)	526(10)[a]	-	380(10)[a]	370-410
Tufted Puffin, Gulf of Alaska Baird and Gould 1983	57°N[a]	47	792(27)[a]	67(110)	600(27)[a]	564(25)[a]
Tufted Puffin, Triangle Island, B.C. Vermeer and Cullen 1979	51°N	43(30)[b] 51(4)[c]	746(27)	63(50)[d]	580(23)[b]	522(23)[b]
Rhinoceros Auklet, Triangle Island, B.C. Vermeer and Cullen 1979	51°N	51(27)[b] 56(9)[c]	520(48)	52(17)[d]	377(27)[b]	361(27)[b]
Rhinoceros Auklet, Destruction Island, Washington Leschner 1976	48°N	51(37)[b] 54(19)[c]	521(51)	-	353(51)[b]	339(51)[b]

[a] Ugaiushak Island, Wehle 1983
[b] good year of growth
[c] marginal year of growth
[d] author, unpubl. data

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Appendix 1. Body weights of nestling Cassin's Auklets, Frederick Island, 1980 and 1981.

Age in days	1980 Number of nestlings	1980 Mean and SD(g)	1980 Range (g)	1981 Number of nestlings	1981 Mean and SD(g)	1981 Range (g)
0	8	20.8± 1.0	20.0- 22.5	15	20.1± 1.8	17.0- 22.5
1	18	24.3± 1.7	20.5- 27	29	22.8± 2.4	14.0- 26.5
2	24	27.5± 2.1	23.0- 32	42	26.8± 3.3	14.0- 34
3	27	31.8± 3.5	24.0- 38.5	43	31.7± 4.2	15.5- 41.5
4	44	36.0± 4.0	27.5- 45	47	36.9± 5.5	18.0- 48
5	48	40.2± 3.8	31.0- 47.5	51	41.1± 6.2	19.5- 58
6	51	45.0± 7.1	31.5- 63	51	45.2± 6.5	24.0- 62
7	48	46.3± 6.8	36.0- 61	52	47.7± 6.6	26.0- 62
8	50	51.2± 9.3	37.0- 78.5	52	52.6± 8.0	27.5- 68.5
9	47	53.0± 8.5	37.0- 82.5	52	58.1±11.6	27.5-101.5
10	45	60.1± 7.1	43.0- 78.5	51	61.0± 9.1	28.0- 78
11	43	63.8±10.4	42.0- 88.5	52	69.4±14.2	27.5-108
12	44	72.5±10.4	52.5-111	50	74.4±11.8	28.0-106.5
13	41	74.4±13.0	51.0-111	50	80.4±14.5	16.5-114
14	41	85.4±15.4	58.5-117	50	87.0±16.6	26.5-120
15	38	92.1±15.6	64.5-120	51	93.8±16.6	25.0-117.5
16	36	99.8±15.1	65.5-128	51	98.7±16.3	29.5-124
17	37	107.7±15.5	75.5-137	51	106.1±17.7	31.5-140
18	31	114.0±15.0	79.0-148	51	111.8±18.5	38.5-150.5
19	38	122.2±12.5	91.0-155	51	118.1±18.8	39.0-152
20	32	125.6±14.0	95.0-159	51	124.8±18.9	43.5-156
21	37	136.8±15.0	101.0-173	51	129.9±18.3	49.5-164
22	29	136.2±14.5	96.0-167	51	131.5±26.7	55.0-161.5
23	35	146.5±14.7	109.0-189	51	139.9±22.7	55.5-172.5
24	26	151.5±14.3	128.0-192	51	145.3±17.0	66.5-178
25	32	158.9±14.9	117.0-192	50	151.6±20.0	66.5-192.5
26	28	164.5±13.8	133.0-194	50	157.4±18.2	80.0-189.5
27	30	165.4±15.4	124.0-195	50	159.1±21.0	64.5-190.0
28	31	173.7±13.1	145.0-203	50	162.3±20.1	68.0-190.0
29	28	171.9±15.8	134.0-200	49	165.6±19.7	81.0-205
30	31	178.6±14.5	151.0-214	50	168.2±18.5	98.0-208
31	30	180.9±15.2	141.0-207	50	172.6±19.4	99.0-228
32	31	182.0±15.7	160.0-226	50	175.6±19.6	103.0-218
33	30	186.7±15.0	161.0-226	50	176.7±26.0	107.0-222
34	33	186.9±18.4	154.0-220	49	183.5±19.5	114.0-214
35	29	191.3±15.7	150.0-214	49	185.4±20.4	124.0-225
36	34	189.2±19.7	147.0-228	50	186.8±21.2	120.0-234
37	30	191.8±17.7	151.0-226	50	188.0±20.3	129.0-231
38	36	191.6±21.0	141.0-222	49	190.6±19.0	124.0-232
39	31	194.1±19.6	152.0-225	48	189.5±19.4	124.0-238
40	35	193.0±19.7	142.0-234	48	189.6±20.0	121.0-243
41	32	190.0±21.3	141.0-230	45	187.9±22.6	112.0-237
42	35	191.5±21.3	141.0-229	42	185.4±20.4	153.0-224
43	27	186.2±15.7	139.0-211	37	174.1±32.6	128.0-214
44	28	187.6±15.5	144.0-221	24	176.9±16.5	150.0-206
45	16	180.2±16.4	139.0-202	14	175.6±14.1	149.0-201
46	17	182.2±17.0	136.0-209	7	174.9±10.9	164.0-192
47	-	-	-	6	174.8±13.0	160.0-191
48	-	-	-	6	170.4±11.8	153.0-185

Appendix 2. Seasonal differences in growth of nestling Cassin's Auklets on Frederick Island, 1980 and 1981.

Age in days	1980						1981					
	May 9-18		May 19-June 1		June 2-23		May 19-June 1		June 2-8		June 9-23	
	N	Mean (g)	N	Mean (g)	N	Mean (g)	N	Mean (g)	N	Mean (g)	N	Mean (g)
0	1	22.5	7	20.5	0	-	3	19.7	10	20.4	2	20.3
1	3	24.5	14	24.0	1	25	10	23.8	14	22.2	5	22.5
2	5	28.0	16	27.0	3	28.5	13	26.9	17	26.2	8	27.6
3	7	33.0	20	31.5	0	-	15	31.2	19	31.6	10	31.7
4	10	38.0	28	35.0	6	37	16	36.2	22	36.5	9	37.8
5	12	41.0	32	40.0	3	41.5	17	40.7	25	40.9	9	43.0
6	14	46.5	30	43.5	6	48.5	17	44.4	25	44.6	9	47.3
7	14	50.5	29	45.0	4	44.5	18	48.9	25	46.8	9	48.1
8	14	54.5	29	49.0	6	56	18	52.8	25	52.2	9	52.8
9	14	55.5	27	50.0	5	64.5	18	58.4	25	55.0	9	65.6
10	14	62.5	24	58.0	6	63	17	60.8	25	60.3	9	62.7
11	14	67.5	24	60.0	5	72.5	18	70.9	25	67.3	10	69.8
12	14	76.0	23	69.5	6	78	17	72.9	24	74.1	9	76.8
13	14	81.0	22	68.0	5	84	17	80.5	24	78.3	9	84.8
14	14	89.5	20	80.5	6	94.5	17	85.5	25	84.3	9	94.0
15	14	97.5	17	83.5	7	102.5	18	94.1	25	91.7	9	100.3
16	14	102.0	15	94.5	6	111	18	100.2	25	95.2	9	104.7
17	14	107.5	16	104.0	7	117.5	18	107.3	25	104.0	9	113.2
18	14	115.0	10	109.0	6	124.5	18	113.7	25	107.4	10	117.7
19	14	120.0	16	120.5	8	129.5	18	120.0	25	114.4	9	125.3
20	13	124.0	13	121.5	6	137.5	18	127.1	25	120.5	9	134.3
21	12	134.0	16	134.5	9	144	18	131.5	25	126.8	9	132.9
22	12	132.5	11	133.5	6	149	18	135.9	25	132.9	9	139.9
23	10	142.0	16	144.5	9	155.5	18	142.3	25	139.1	9	147.3
24	9	149.5	11	149.5	6	159	18	147.2	25	142.8	10	150.8
25	9	151.0	14	160.0	9	165	18	149.8	25	149.9	9	159.2
26	8	162.5	13	164.0	7	167.5	17	156.8	25	155.7	10	156.6
27	8	161.0	13	163.5	9	172	18	159.9	25	158.7	9	157.2
28	7	171.0	16	175.0	8	173.5	18	162.1	24	160.4	9	162.7
29	6	172.0	13	169.0	9	176	18	168.4	25	164.2	9	165.4
30	6	184.5	16	177.5	9	176.5	18	172.7	25	165.5	9	166.4
31	7	180.5	13	182.5	10	179	18	174.3	25	173.9	9	169.8
32	5	183.0	16	185.0	10	177	17	175.2	25	176.7	9	170.8
33	6	196.5	13	186.5	11	181.5	17	179.2	24	181.3	9	172.6
34	7	189.0	16	189.5	10	181	17	182.5	24	185.7	9	174.0
35	6	199.0	13	191.5	10	186.5	17	186.6	24	188.8	9	168.3
36	7	197.0	16	190.0	11	183	18	190.5	24	191.5	8	162.6
37	5	202.5	14	194.0	11	184.5	18	192.2	24	191.7	8	166.3
38	7	201.0	19	192.5	10	183	18	195.6	24	192.1	7	171.4
39	6	209.0	16	194.0	9	185	18	195.3	24	193.0	7	168
40	7	203.5	20	194.5	8	181	18	195.9	24	190.7	7	168.3
41	6	204.5	18	192.0	8	175	17	193.8	24	186.9	5	161.8
42	7	204.5	21	192.5	7	175.5	18	188.8	20	184.5	5	170.2
43	6	194.5	16	185.0	5	179	15	189.5	20	171.3	3	171.3
44	6	196.5	19	186.5	3	176.5	12	185.7	11	167.9	2	166.0
45	3	184.5	11	181.0			7	185.0	6	144.3		
46	5	187.0	10	182.5			6	179.2				
47			6	182.0			4	180.8				
48			5	184.0			4	173				

Appendix 3. Morning and evening weights of Rhinoceros Auklets, Triangle Island, 1978

Age in days	Number of nestlings	Mean morning weight (0800 PST) & SD(g)	Number of nestlings	Mean evening weight (2000 PST) & SD(g)
0	5	51.0 ± 1.4	-	-
1	5	60.8 ± 10.0	4	60.8 ± 5.8
2	6	66.8 ± 12.4	4	67.3 ± 13.4
3	8	74.9 ± 10.4	6	68.2 ± 14.1
4	11	84.2 ± 16.2	10	75.3 ± 16.4
5	11	91.3 ± 22.3	11	82.5 ± 17.5
6	13	103.1 ± 21.0	13	92.7 ± 19.5
7	14	106.7 ± 22.7	14	97.9 ± 20.3
8	14	119.5 ± 24.2	13	103.4 ± 22.5
9	15	123.1 ± 21.6	15	112.2 ± 21.4
10	16	136.4 ± 25.3	16	121.6 ± 22.1
11	17	146.5 ± 25.6	17	131.5 ± 21.1
12	17	150.4 ± 31.2	17	137.9 ± 27.8
13	17	166.4 ± 29.8	17	149.5 ± 27.4
14	18	187.1 ± 52.6	18	169.2 ± 49.3
15	19	191.7 ± 49.4	18	171.3 ± 41.1
16	19	204.8 ± 48.9	19	185.7 ± 47.3
17	19	209.2 ± 48.3	19	192.4 ± 49.5
18	19	218.6 ± 52.4	18	200.3 ± 50.7
19	19	225.4 ± 50.6	19	207.6 ± 48.0
20	19	235.4 ± 45.9	19	218.1 ± 48.5
21	19	241.3 ± 39.8	18	222.6 ± 36.7
22	19	246.8 ± 39.3	19	229.8 ± 34.7
23	19	250.4 ± 40.3	19	238.4 ± 52.0
24	19	262.4 ± 41.0	19	239.9 ± 38.0
25	19	266.2 ± 38.4	15	248.1 ± 38.8
26	19	272.5 ± 42.6	18	250.0 ± 37.9
27	19	282.0 ± 43.1	19	261.4 ± 41.3
28	19	282.6 ± 44.1	18	263.4 ± 40.0
29	19	289.3 ± 42.3	18	270.3 ± 42.4
30	18	292.0 ± 44.4	15	269.3 ± 39.4
31	19	302.7 ± 39.6	17	287.6 ± 41.1
32	19	309.8 ± 41.2	19	289.4 ± 42.2
33	19	313.7 ± 41.4	17	294.1 ± 42.2
34	19	311.0 ± 47.2	17	297.7 ± 45.7
35	19	316.6 ± 54.8	19	295.0 ± 53.3
36	19	314.8 ± 53.7	19	297.7 ± 51.5
37	18	324.9 ± 50.4	19	301.1 ± 50.8
38	18	321.3 ± 57.9	17	300.3 ± 53.3
39	16	332.4 ± 48.9	19	307.3 ± 48.6
40	18	324.7 ± 48.4	19	308.5 ± 47.6
41	19	327.1 ± 46.0	16	318.6 ± 44.8
42	19	340.4 ± 48.7	17	321.5 ± 47.1
43	17	349.1 ± 43.3	17	323.7 ± 42.0
44	14	344.8 ± 38.4	16	327.8 ± 42.7
45	15	349.8 ± 47.6	15	342.2 ± 42.6
46	16	350.3 ± 42.6	14	333.4 ± 39.9
47	13	343.2 ± 45.2	14	334.4 ± 45.3
48	13	351.5 ± 47.3	14	333.4 ± 45.7
49	14	349.1 ± 37.9	14	330.8 ± 39.4
50	11	353.4 ± 41.0	11	328.5 ± 39.2
51	9	332.9 ± 38.1	9	319.9 ± 36.3
52	7	335.6 ± 48.7	7	318.3 ± 41.7
53	5	326.6 ± 39.3	5	314.0 ± 40.0
54	2	332.0 ± 17.0	2	312.0 ± 10.0

Appendix 4. Body weights of nestling Tufted Puffins, Triangle Island, 1978

Age in days	Number of nestlings	Mean & SD(g)	Range (g)
0-1	16	68.1 ± 6.9	55- 78
2-3	25	81.1 ± 11.1	64-113
4-5	32	111.1 ± 13.2	83-138
6-7	31	143.0 ± 15.8	123-172
8-9	35	179.6 ± 24.7	105-231
10-11	34	221.9 ± 28.8	174-292
12-13	34	251.7 ± 34.6	147-323
14-15	36	293.5 ± 37.1	155-377
16-17	32	340.8 ± 43.9	194-452
18-19	36	378.8 ± 44.7	265-472
20-21	32	410.0 ± 43.6	322-504
22-23	35	428.8 ± 40.0	366-520
24-25	30	450.8 ± 41.9	331-520
26-27	29	488.9 ± 44.4	404-596
28-29	33	489.7 ± 52.8	406-596
30-31	29	507.8 ± 47.7	416-595
32-33	28	520.1 ± 51.8	425-620
34-35	26	527.9 ± 51.3	420-626
36-37	29	540.8 ± 53.8	459-647
38-39	28	548.1 ± 61.2	461-676
40-41	24	544.7 ± 51.0	433-635
42-43	17	536.6 ± 51.1	450-633
44-45	7	521.4 ± 35.8	468-577